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Cetorhinus cf. *C. maximus* (Gunnerus) (Lamniformes: Cetorhinidae), A Basking Shark from the Late Miocene Empire Formation, Coos Bay, Oregon

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Abstract.—The family Cetorhinidae Gill includes one extant genus, *Cetorhinus* Blainville, and a single living species, the basking shark, *C. maximus* (Gunnerus). Basking sharks are coastal pelagic to oceanic with circumglobal distribution in boreal to warm-temperate waters of the continental and insular shelves. Second only in size to the whale shark, *Rhincodon typus*, basking sharks attain a maximum total length of 12 to 15 m (although generally not exceeding 9.8 m), and are planktivorous, feeding by filtering copepods, barnacles, decapod larvae and fish eggs from the water. The first Tertiary records of undisputed cetorhinids are from the middle Eocene of Antarctica, possibly the middle Eocene of Russia, and the late Eocene of Oregon. Eocene cetorhinids are referred to *Keasius taylori*, and Oligocene through early Miocene basking sharks are traditionally assigned to *Keasius parvus*. The earliest occurrence of *Cetorhinus* in the northeastern Pacific is early Miocene, and fossils attributed to this genus are relatively common in middle Miocene through Pleistocene marine sediments of Oregon, California, and Baja California, Mexico. Late Miocene and younger *Cetorhinus* are conventionally placed in the extant species, *C. maximus*. Late Miocene fossils of a basking shark from the Coos Conglomerate Member of the Empire Formation, Oregon, were collected in 1972 by students from the University of California, Berkeley. Associated vertebrae and gill rakers compare favorably in size and overall morphology with those of adult Recent *C. maximus*. Based on correlations of vertebral and gill raker dimensions with the total length for Recent *C. maximus*, the Empire basking shark is estimated to have been between 4.5 and 5.75+ m in total length. Although gill rakers and vertebrae from the Empire Formation compare favorably with those of *C. maximus*, a definitive identification requires dentition. The occurrence of *Cetorhinus cf. C. maximus* in the late Miocene of Oregon is consistent with other late Miocene records of this species in California and Chile. *C. maximus* may range no earlier than late Miocene in the eastern North Pacific.

Introduction

The Family Cetorhinidae Gill, 1862, includes one extant genus, *Cetorhinus* Blainville, 1816, and a single living species, the basking shark, *C. maximus* (Gunnerus, 1765) (Springer and Gilbert, 1976; Compagno, 1984, 2001). Basking sharks are among the largest living neoselachians, exceeded only in size by the whale shark *Rhincodon typus* (Smith, 1828), attaining a maximum total length of 12.2 to 15.2 m, although generally not exceeding 9.8 m in total length (Compagno, 2001). *Cetorhinus maximus* is also characterized by having large gill slits that nearly encircle the head, numerous long, filamentous dermal denticle gill rakers lining the anterior and posterior sides of each branchial arch, a strongly pointed snout and large subterminal mouth with numerous small, monocuspid teeth, strong lateral keels on the caudal peduncle and a large lunate caudal fin (Compagno, 2001).

The living basking shark is coastal pelagic to oceanic with a circumglobal distribution in boreal to warm-temperate waters of the continental and insular shelves; it occurs both offshore and in shallow coastal waters and enters enclosed bays (Compagno, 2001). In the northeastern Pacific, *Cetorhinus maximus* ranges from the Gulf of California, northern Mexico to the Gulf of Alaska and perhaps the Aleutian Island chain (Mecklenburg et al., 2002; Lamb and Edgell, 2010). Basking sharks are planktivorous, feeding by filtering copepods, barnacles, decapod larvae, and fish eggs from the water (Compagno, 2001). They feed, while swimming slowly with their mouths wide-open, allowing water and plankton to pass through the buccal cavity, into the pharynx and across the branchial arches, which are lined with numerous gill rakers (1260 gill rakers per gill: Bigelow & Schroeder, 1948, p. 150; Matthews and Parker, 1950, p. 564). Plankton are sieved out as the water passes between the gill rakers and is expelled through external gill openings. Matthews and Parker (1950) suggest that mucous excreted along the base of the gill rakers aids in the capture of food.

The Family Cetorhinidae includes two extinct genera, *Pseudocetorhinus* Duffin, 1998, and *Keasius* Welton, 2013. Teeth and gill rakers of *P. pickfordi* Duffin, 1998, were originally described from the Rhaetian of England and also occur in the Late Triassic of France (Cuny et al., 1994; Cuny, 1995; Cuny et al., 2000), Belgium (Cuny et al., 1994) and Luxembourg (Godefroit et al., 1998). According to Duffin (1998), *P. pickfordi* may represent the earliest known cetorhinid and the first filter-feeding shark. Allocation of *Pseudocetorhinus* to the Cetorhinidae is not particularly convincing, and probably has no phylogenetic relationship with Tertiary and Recent Cetorhinidae. A gap in the fossil record of the Cetorhinidae exists from the Early Jurassic through early Eocene, with the first Tertiary records of undisputed cetorhinids in the middle Eocene of Antarctica (Cione and Ruguero, 1998), the Eocene of Oregon (Welton *in* Cappetta, 1987, p. 107; Welton, 2013), and possibly the middle Eocene of Russia (Malyshkina, 2006).

There are approximately six nominal extinct cetorhinid species, ranging in age from the middle Eocene to late Pleistocene (Cappetta, 2006; Welton, 2013). Of these six species, three (*Cetorhinus duponti* (Hasse, 1882) and *C. selachoides* (Hasse, 1882), both from the early Pliocene of Anvers, Belgium, and *C. glauconiticus* (Noetling, 1885), from the upper Rupelien (Oligocene) of Russia) are based on vertebrae. Two species (*Keasius parvus* (Leriche, 1908), from the upper Rupelian (Oligocene) Boom Clay of Belgium, and *C. auratus* (Van Beneden, 1871, from the early Pliocene of Anvers, Belgium) are based on gill rakers, and *K. taylori* Welton, 2013, was recently described from an associated skeleton with teeth, vertebrae and gill rakers. The validity of *C. glauconiticus* and *C. selachoides* is questionable (Cappetta, 2006), and *C. duponti* and *C. auratus* are junior synonyms of *C. maximus* (Woodward, 1889; Leriche, 1908, 1921; Cappetta, 2006). *Keasius parvus* is a valid Oligocene through perhaps early Miocene species, and *K. talyori* is known from the middle and late Eocene.

Conventionally, almost all late Miocene and younger cetorhinids are referred to *Cetorhinus maximus*, and early Miocene and Oligocene basking sharks are assigned to *Keasius parvus*. A proximal gill raker referred to *Cetorhinus* sp. from the middle Eocene La Meseta Formation of Seymour Island, Antarctica (Cione and Reguero, 1998), was referred to *C. parvus* by Hovestadt and Hovestadt-Euler (2011), and has subsequently been assigned to *K. taylori* (Welton, 2013).

Oligocene occurrences of *Keasius parvus* include Germany (Weiler, 1922, 1928, 1931; Leriche, 1948; Muller, 1976, 1983; Von Der Hocht, 1978a, 1978b; Pfeil, 1981; Freess, 1991, 1992; Reinecke et al., 2001, 2005; Haye et al., 2008; Gille et al., 2010; Hovestadt et al., 2010; Hovestadt and Hovestadt-Euler, 2011; De Pietri et al., 2010), Belgium (Leriche, 1908, 1910; Herman, 1979; Van Den Bosch, 1984; Baut and Genault, 1999), Switzerland (Frohlicher and Weiler, 1952), France (Dutheil, 1991; Baut, 1993; Genault, 1993; Pharisat, 1998; Merle et al., 2002), and questionably identified from a placoid scale from South Carolina, U.S.A. (Cicimurri and Knight, 2009). *Cetorhinus* sp. has been reported from the late Oligocene of Japan (Uyeno et al., 1984; Yabumoto and Uyeno, 1994), and Baja California, Mexico (Gonzalez-Barba and Thies, 2000). Indeterminate fragmentary cetorhinid gill rakers occur in the Oligocene Kirker Formation of California (Welton, unpublished data).

Miocene occurrences of *Keasius parvus* include Germany (Kruckow, 1961; Barthelt et al., 1991; Bracher and Unger, 2007; Reinecke et al., 2008, 2011), Switzerland (Bolliger et al., 1995), Austria (Brzobohaty and Schultz, 1978; Schultz, 1978; Schmid et al., 2001), and France (Vialle et al., 2011).

Unidentified Oligocene species of *Cetorhinus* are reported from Romania (Jonet, 1947), Poland (Van Den Bosch, 1981; Bienkowska-Wasiluk and Radwanski, 2009), and Japan (Kikuchi and Takaoka, 1979; Tomita and Oji, 2010). Early to middle Miocene basking sharks are quite diverse, largely unstudied, and usually referred to *Cetorhinus* sp. (Applegate *in* Mitchell and Tedford, 1973; Domning, 1978; Karasawa, 1989; Yabumoto and Uyeno, 1994; Bolliger et al., 1995; Gottfried, 1995; Purdy et al., 2001; Gonzalez-Barba and Thies, 2000) or are variously assigned to *C. maximus* (Brzobohaty and Schultz, 1978; Karasawa, 1989; Uyeno et al., 1983; Yabumoto and Uyeno, 1994; Long, 1994). Jordan and Hannibal (1923, p. 31, pl. III-B and I, but not C-F, L-M, Q, W, and CC) figure two *Cetorhinus* teeth from California (most likely from the middle Miocene – Barstovian, Round Mountain Silt) under the genus *Gyrace* Jordan, 1923, a junior synonym of *Galeocerdo* Muller and Henle, 1837. Gonzalez-Barba and Thies (2000) report *Cetorhinus* sp. from the Tortonian of Baja California, Mexico and *Cetorhinus* sp. occurs in the late Miocene-early Pliocene of Holland (Wijnker et al., 2008), and the late Miocene (Stewart, 1997; Barnes, 2008) and Pliocene (Applegate, 1978) of Baja California, Mexico. Almost all late Miocene through Pleistocene basking sharks are included in *C. maximus,* with occurrences in Belgium (Herman et al., 1974; Herman, 1979; Nolf, 1986; Van Der Brugghen, 2005), Italy (Lawley, 1876; Landini, 1977; Marsili, 2008; Cigala-Fulgosi et al., 2009), France (Cappetta and Nolf, 1991), Japan (Uyeno and Matsushima, 1974), the Czech Republic (Schultz et al., 2010), Chile (Long, 1993), California (Kanakoff, 1956; Fitch, 1970; Langenwalter, 1975; Long, 1994; Boessenecker, 2011), Oregon (Long, 1994; Welton, unpublished data), and Baja California, Mexico (Long, 1994).

In the summer of 1972, students of the University of California at Berkeley, Summer Institute, discovered associated skeletal elements of a basking shark in the Coos Conglomerate Member of the Empire Formation at Fossil Point, Coos Bay, Oregon (Fig. 1). The specimen was collected in a calcareous sandstone concretion and consists of three vertebrae and 11 fragmentary gill rakers. This paper describes the Empire Formation *Cetorhinus* fossils and compares them with vertebrae and gill rakers of the recent basking shark *C. maximus*. This paper is the second in a series of studies to document the taxonomy and stratigraphic distribution of Tertiary eastern North Pacific cetorhinids.

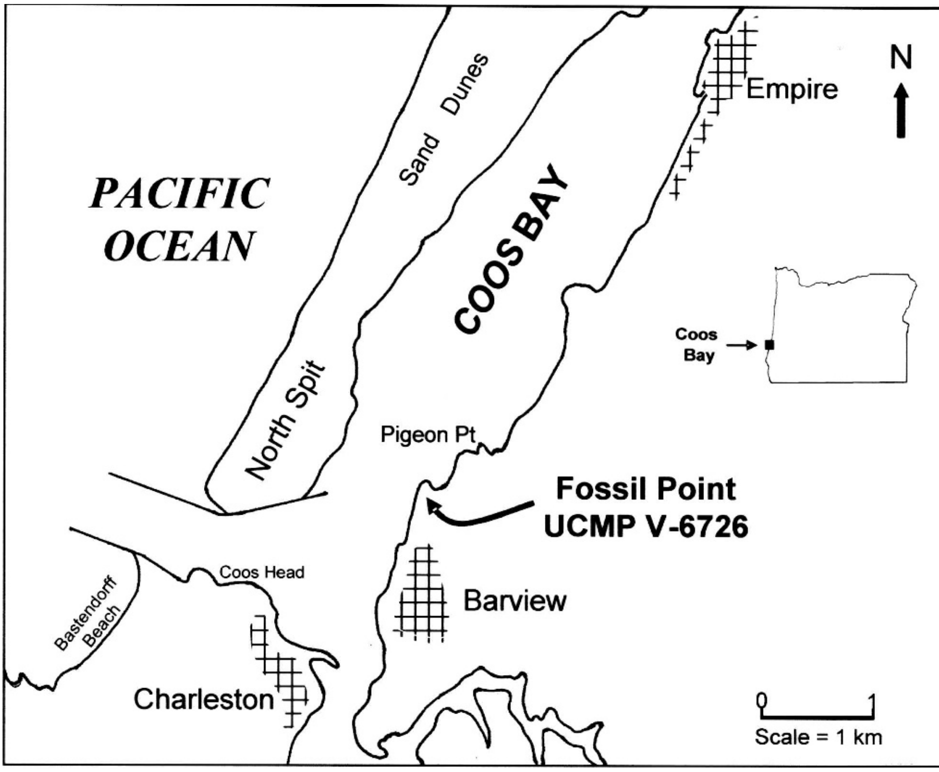

Fig. 1. Map of Coos Bay, Oregon showing location of Fossil Point and UCMP locality V-6726, in the Coos Conglomerate Member of the late Miocene Empire Formation.

Material and Methods

Modern and fossil specimens described or referenced in this study are housed in scientific institutions in the United States and the Netherlands as indicated by the following acronyms:

KBIN - Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels, Belgium

LACM - Natural History Museum of Los Angeles County, Los Angeles, California, U.S.A.

UCMP - University of California, Museum of Paleontology, Berkeley, California, U.S.A.

The terminology for individual gill rakers (Fig. 2) has been modified from Hovestadt and Hovestadt-Euler (2011), and follows Welton (2013). Anatomical terms for vertebral centra and their internal calcifications are derived from Ridewood (1921), Wintner and Cliff (1999), Wintner (2000).

The fossils of *Cetorhinus* cf. *C. maximus* (UCMP 77642, locality UCMP V-6726), are catalogued and housed in the Museum of Paleontology, University of California, Berkeley, and precise locality data for this specimen may be obtained from the same institution. Detailed descriptions and illustrations of gill rakers of extant *C. maximus* are found in Van Den Bosch (1984), Hovestadt-Hovestadt-Euler (2011), and Welton (2013). Comparisons with the Empire basking shark are also based on examination of the following specimens: *C. maximus*, LACM 35876-1, wet-preserved gill arch with gill

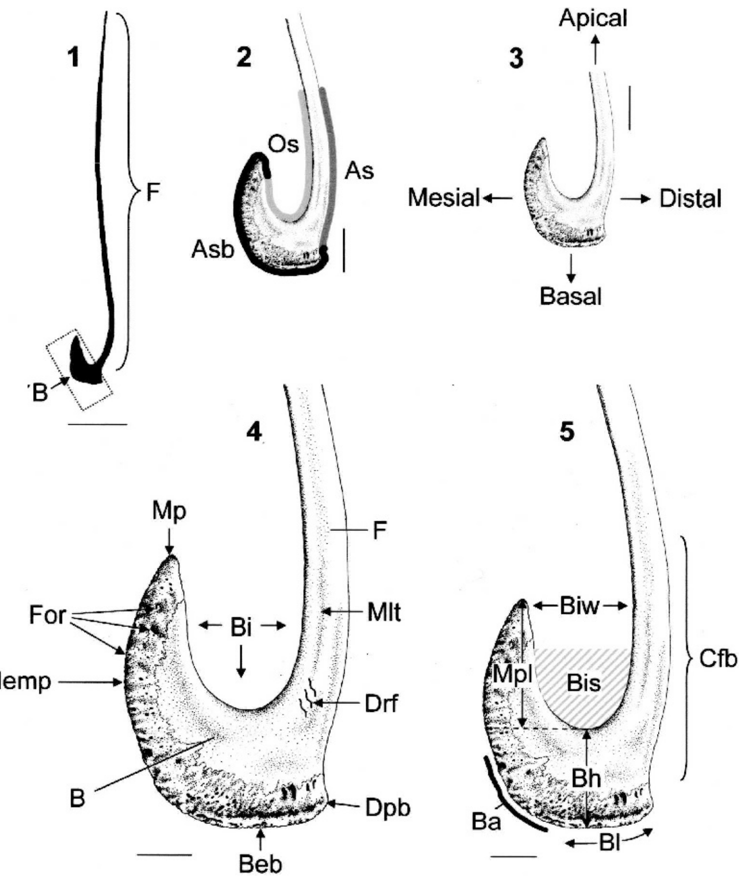

Fig. 2. Cetorhinid gill raker terminology. *Cetorhinus maximus*, LACM 35876-1, adult male, 6.0–6.7 m (TL). (1) Major gill raker components. (2) Gill raker surfaces; oral surface - light gray, aboral surface – dark gray, attachment surface of base – black. (3) Gill raker orientation terms. (4) Gill raker morphologic terms. (5) Gill raker measurements. **Abbreviations**: **As** – aboral surface; **Asb** – attachment surface of base; **B** – base of gill raker; **Ba** – base angle; **Beb** – basal edge of base; **Bh** – base height; **Bi** – bight; **Bis** – bight shape; **Biw** – bight width; **Bl** – basal length of base; **Cfb** – curvature of filament base; **Dpb** – distal protuberance of base; **Drf** – diagonal ridges on filament; **F** – filament; **For** – foramina of attachment surface; **Memp** – mesial edge of medial process; **Mlt** – median longitudinal trough; **Mp** – medial process; **Mpl** – medial process length; **Os** – oral surface. Scales: (1) = 5 mm; (2–3) = 4 mm; (4–5) = 2 mm.

rakers, adult male, 6.0–6.7 m total length (TL), collected off Morro Bay, San Luis Obispo, California, 30 June 1976. Descriptions and illustrations of gill rakers belonging to the Oligocene *Keasius parvus* are found in Leriche (1910) and Hovestadt-Hovestadt-Euler (2011). Comparisons were also made with *K. parvus* gill rakers based on LACM 154925, 20 gill rakers from LACM Locality 3813, Oligocene (Rupelien), U. Meeressand, Weinheim bei Alzey Steinbruch an der Neumuhle.

The associated skeletal elements are preserved in a calcareous concretion, and were initially prepared by etching in a weak (5%) acetic acid solution to expose gill rakers and calcified vertebral cartilages. Additional preparation was done with an air abrasive unit. All artwork and photographs are by the author. The illustrations in Figures 2 and 6 were drawn using a Wild M5 stereomicroscope and camera-lucida attachment.

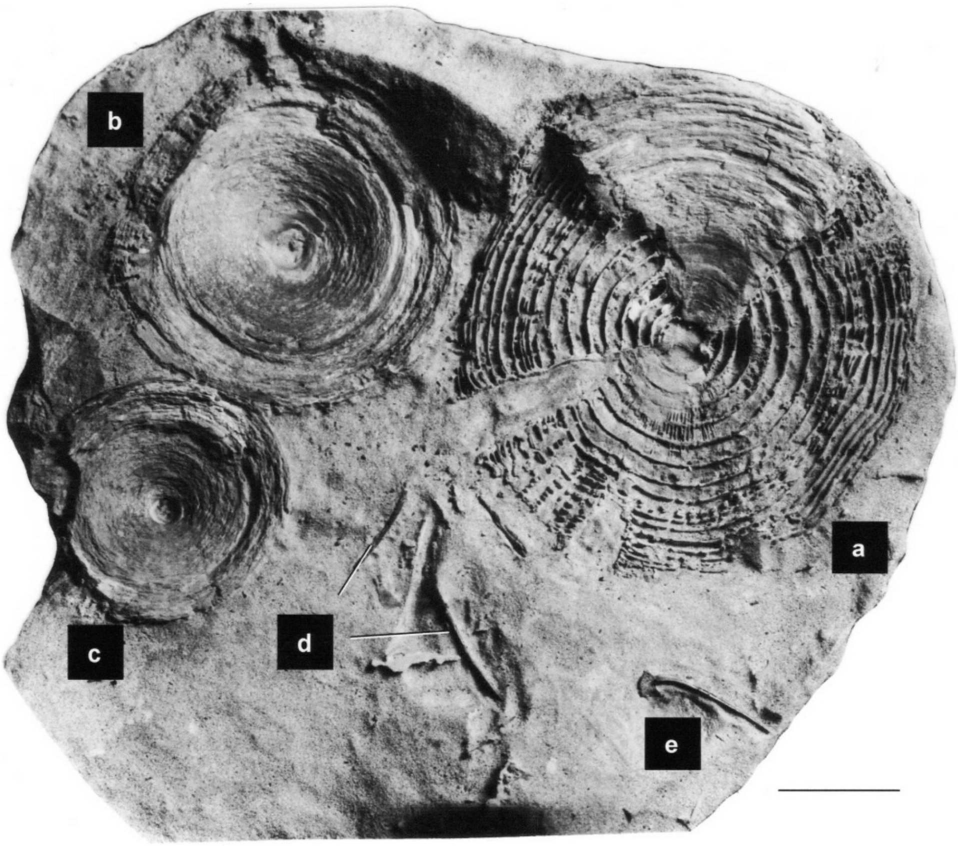

Fig. 3. Acid etched calcareous concretion from the Coos Conglomerate Member of the Empire Formation (UCMP Locality V-6726, Fossil Point, Coos County, Oregon) with exposed vertebrae and gill rakers of *Cetorhinus* cf. *C. maximus* (UCMP 77642). a, transverse section of abdominal or trunk vertebra showing concentric calcifications of intermedialia; b, axial view of intermediate sized vertebra showing the corpus calcareum and radial calcifications on broken surface (upper left margin of centrum); c, axial view of caudal? vertebra with exposed radial calcifications; d, fragmentary gill raker filaments; e, incomplete gill raker with a well preserved base. Scale = 2 cm.

Systematic Paleontology

Class Chondrichthyes Huxley, 1880

Superorder Galeomorphii Compagno, 1973

Order Lamniformes Berg, 1958

Family Cetorhinidae Gill, 1862

Genus *Cetorhinus* Blainville, 1816

Cetorhinus cf. *C. maximus* (Gunnerus, 1765)

Figs. 3a-e, 4–6a-d

Referred Specimen—UCMP 77642, three vertebrae, and 11 fragmentary gill rakers (Figs. 3–6).

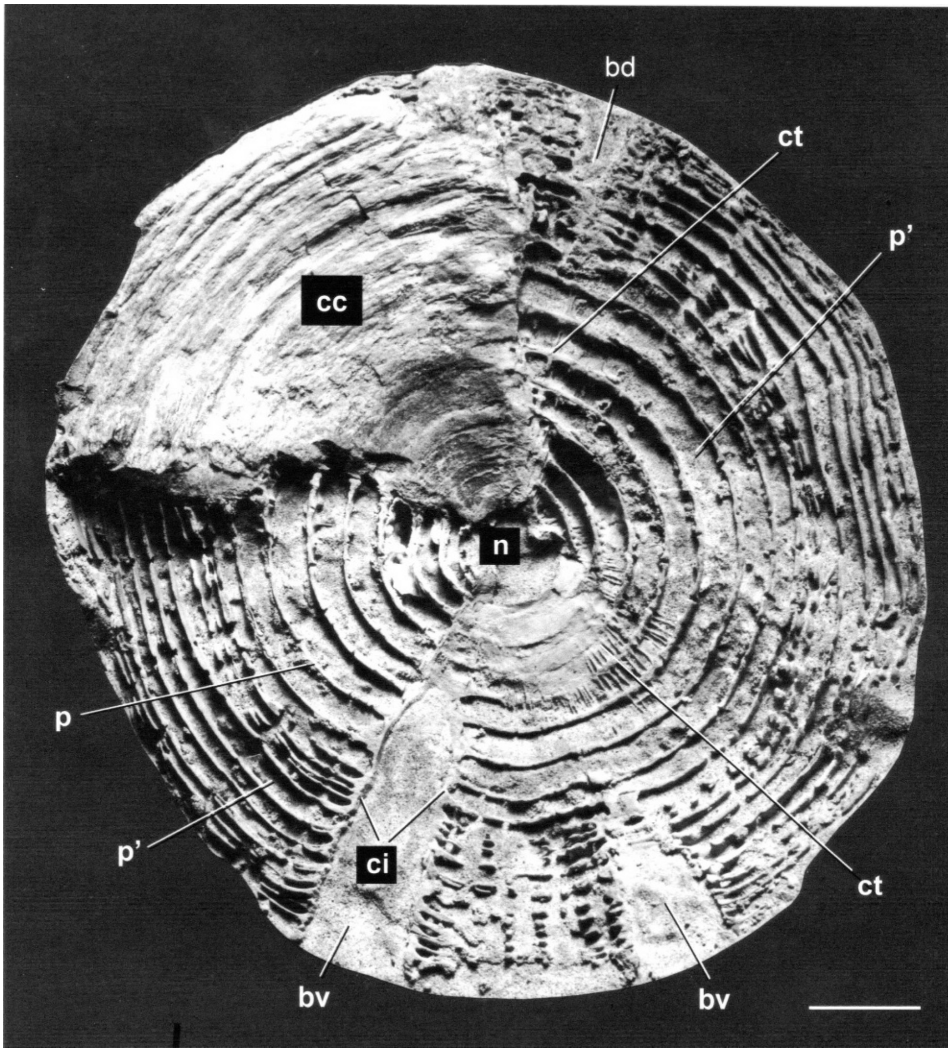

Fig. 4. Acidized transverse section through largest vertebra of *Cetorhinus* cf. *C. maximus* (UCMP 77642), showing calcifications of the intermedialia. **Abbreviations**: **bd** - basidorsal insertion; **bv** - basiventral insertion; **cc** - corpus calcareum; **ci** - calcified wedge face of intermediale; **ct** - calcified tube; **n** - passage of notochord; **p** - uncalcified cartilaginous part of the intermediale; **p′** - calcified concentric lamellae of the intermediale. Scale = 1 cm.

Locality—UCMP V-6726, Fossil Point, Coos County, Oregon, approximately 900 meters southwest of Pigeon Point and about 2400 meters north of Charleston, Coos County, Oregon (Fig. 1).

Formation—UCMP 77642 was collected from the Coos Conglomerate Member of the Empire Formation (Diller, 1896; Dall, 1898, 1909; Howe, 1922; Weaver, 1945; Armentrout, 1973, 1980). The Coos Conglomerate is composed of cobbles and boulders of fossiliferous lower Empire Formation sandstone, rounded beach pebbles and cobbles of chert, basalt, quartzite, and reworked Empire Formation fossils mixed with contemporaneous shallow water fauna (Armentrout, 1973, p. 4). Dall (1909) was able

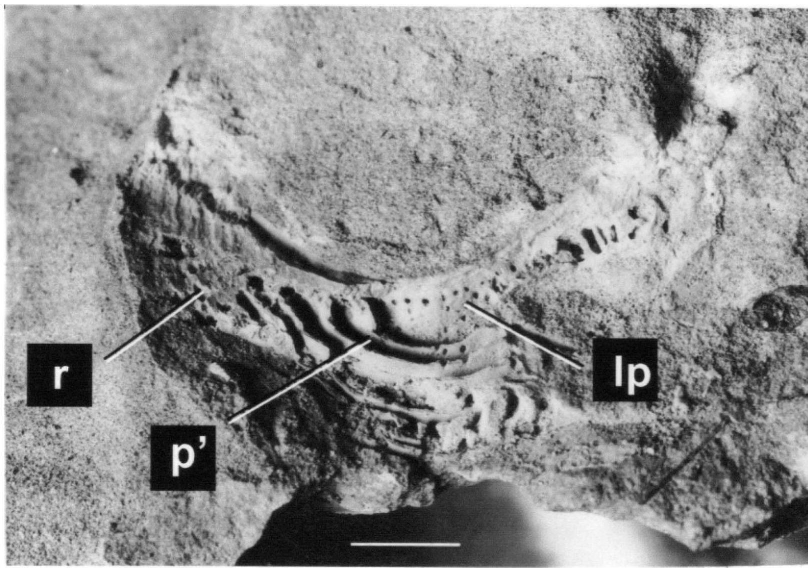

Fig. 5. Exposed concentric lamellae (p′) along broken section of *Cetorhinus* cf. *C. maximus* vertebrae (UCMP 77642, Fig. 3c) showing numerous perforations (lp), and radial calcifications (r). Scale = 1 cm.

to make a distinction between fossils derived from the underlying Empire Formation sandstone and those deposited contemporaneously with the Coos Conglomerate by carefully noting color and matrix composition. The *Cetorhinus* skeletal elements are contained in a fine to medium grained, gray, calcareous sandstone nodule, surrounded by a matrix of basalt and quartzite pebbles up to 5.0 mm in diameter. Based on similarities in lithology, this nodule was probably reworked from lower Empire Formation sandstone.

Age—Late Miocene, *Thalassiosira antiqua* and possibly the *Nitzschia reinholdii* northeastern Pacific Diatom Zones (Barron and Armentrout, 1980; Barron, 1981, addendum p. 123, p. 124, fig. 7; Armentrout 1981, p. 142, annotations 50 and 51, p. 143, fig. 2), Wishkahan Molluscan Stage (Addicott, 1976, 1981), early part of the Hemphillian North American land-mammal "age" (Repenning *in* Armentrout, 1981, p. 141, annotation 25), and between 6.5 and 8.5 Ma (Armentrout, 1981, p. 143, fig. 2; Armentrout et al., 1983).

Description—The skeletal elements of *Cetorhinus* were first recognized in the field as a series of associated, but disarticulated, calcified centra and gill rakers, weathering *in situ* from the Coos Conglomerate Member of the Empire Formation. The skeleton is preserved in a single calcareous sandstone concretion (Fig. 3), and the association is assumed to represent one individual for the following reasons: 1) all skeletal elements belong to the same taxon; 2) all gill rakers are within a size range found on a single gill arch (Hovestadt and Hovestadt-Euler, 2011, p. 79, fig. 9m-u; Fig. 6), and the three associated centra are within the size range for one individual (Natanson et al., 2008). Evidence of some postmortem transport is indicated by the juxtaposition of vertebrae from different positions along the vertebral column, in combination with scattered gill rakers in the matrix.

Vertebrae—The largest vertebra (Figs. 3a, 4) is seen in transverse section broken midway between the anterior and posterior ends of the centrum. A wedge-shaped section of the corpus calcareum is preserved (Fig. 4) and covers one of the wedge cartilages. The

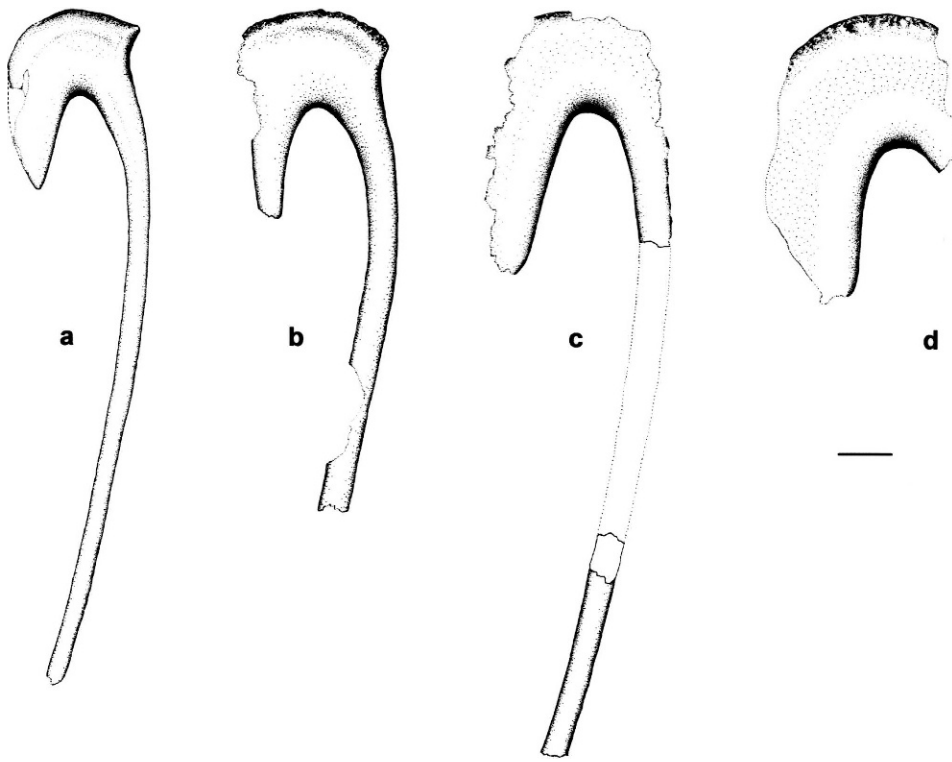

Fig. 6. Incomplete gill rakers of *Cetorhinus* cf. *C. maximus* (UCMP 77642), from the Coos Conglomerate Member of the late Miocene Empire Formation, Coos County, Oregon (UCMP locality V-6726). The gill raker sequence **a** through **d** approximates distal-most to central-most positions on the gill arch. Scale = 2 mm.

centrum is readily differentiated into four intermedialia by the basidorsal and basiventral insertions for the neural and haemal arch cartilages (Fig. 4). Outer zone cartilage of the intermedialia (Ridewood, 1921) contain approximately 20 calcified concentric lamellae, the innermost calcifications being the oldest and the outermost thinner lamellae being most recently calcified. Each lamella bears many sieve-like perforations (Fig. 5) in the lamellar wall, connected to each adjacent concentric lamellar wall by a calcified tube, which during life transmitted a blood vessel (Ridewood, 1921). Each interlamellar tube originates near the innermost concentric lamellae and grows radially toward the perimeter of the centrum. Isolated nodules that occur in the uncalcified wedges of the neural and haemal arch cartilage as seen in modern vertebral cross sections (island or isolated nodules or calcified cartilage of Ridewood, 1921, p. 361) are absent in this specimen. The wedge faces, i.e., the faces which are in contact with arch cartilage are well calcified, a feature that Ridewood (1921:360) suggests is an adult characteristic. Radiating lamellae are absent. The greatest diameter of the centrum, measured to the outside of the last lamellar calcification is approximately 80 mm.

The corpus calcareum of the intermediate-sized vertebra is exposed in axial view. Poorly preserved growth band pairs of alternating ridges and troughs are visible in Figure 3b. Radial calcifications are exposed along the broken perimeter of the centrum. The centrum is 58 mm in transverse width. The smallest centrum is partially broken along one side revealing numerous lamellar perforations (Figs. 3, 5) and radial calcifications. The radii extend from the perimeter of the centrum, inward toward the notochord for a distance of one-half the radius. The centrum is approximately 42 mm in transverse width and 27 mm in anteroposterior length.

Gill Rakers—Eleven fragmentary gill rakers are preserved, four of which have bases (Fig. 6), and the remainder consist of filament sections. The longest incomplete gill raker (Fig. 6c) is 26+ mm. The filaments are gently curved medially, taper apically, are laterally thin, and may have either a weak median longitudinal trough developed just above the point at which the filament connects with the base (Fig. 2), or this surface is flat to weakly convex. The oral and aboral filament surfaces are rounded, and the filaments are widest and most strongly curved at their junction with the base. The base of one gill raker (Fig. 6a) has a well developed distal projection, and basal edges range from flat to moderately rounded (Fig. 6 a, b, d). The medial process is long in all gill rakers, tapers apically with a broad base, and ranges from narrow (Fig. 6b) to somewhat triangular in shape (Fig. 6a). The mesial edge of the medial process is straight (Fig. 6b) to rounded (Fig. 6a, d) and the intersection of the basal edge of the base and the mesial edge of the medial process ranges from angular (Fig. 6b) to subangular (Fig. 6a, d). A narrow, rugose basal attachment surface is continuous from the distal basal projection to the apical tip of the medial process. The bight is subangular in all gill rakers, and the basal height, as measured at the point of greatest bight curvature (Figs. 2, 6) is relatively wide. Except for the basal attachment surface, all gill raker surfaces are covered by smooth to very finely textured enameloid. Broken filament cross sections show a hollow pulp cavity that persists medially throughout the length of the gill raker.

Discussion

Vertebrae—Calcifications in the centra in Recent *Cetorhinus maximus* have been described by Hasse (1882), Ridewood (1921), and illustrated by Natanson et al. (2008, p. 272, fig. 1). The calcifications found in the Empire basking shark (Figs. 3–5) compare favorably with those of *C. maximus* in sharing the following attributes: centrum nearly oval in axial view; diagonal lamellae absent in large trunk vertebrae and present in much small caudal centra; intermedialia weakly calcified with well-developed concentric lamellae; basidorsal and basiventral insertions for the neural and haemal arch cartilages well developed with moderately calcified wedge faces; small tubes radiate from the centrum focus (Wintner and Cliff, 1999), passing through concentric lamellae and extend to the margin of the centrum; primary double cone angle, measured from the focus to the anterior or posterior margin of the corpus calcareum, is high; length of centrum much greater than other lamniforms.

According to Ridewood (1921, p. 361–362), ventral intermediale in trunk vertebrae are wider than the dorsal intermediale. In the cloacal region, they are about equal, and the ventral intermediale continue to narrow in the caudal region. Natanson et al. (2008, p. 272, fig. 1) figured a series of *Cetorhinus maximus* vertebrae representing cranial, abdominal and trunk vertebrae, illustrating a trend from ventrolaterally directed basopophyses in cranial vertebrae, increasing lateral direction in abdominal vertebrae, and a reverse of the trend in trunk vertebrae. The trends noted above are potentially useful in determining the relative position of isolated vertebrae in the vertebral column. Unfortunately, as pointed out by Ridewood (1921), it is not possible with certainty to determine the dorsal orientation of an isolated centrum. As an alternative, one can infer relative position based on vertebral size, if the sample represents an association from one individual. Applying the above criteria, the presence of concentric lamellae and lack of radii in the largest Empire centrum (Figs. 3a, 4) suggests this vertebra is from the trunk region. Although one basopophyses is hidden by a fragment of the corpus calcareum, it appears that one pair is more ventrolaterally directed than the other. On this basis, the centrum illustrated in Figure 4 is oriented with the most laterally directed basopophyses in the ventral position. The smallest Empire centrum (Fig. 3c) possesses radial calcifications on the external surface of the outermost concentric lamellae. A caudal position for this centrum is indicated by its small size, in combination with the presence of radial calcifications.

There are currently no studies documenting individual, ontogenetic, or geographic variations in the vertebrae of Recent *Cetorhinus maximus*. In the absence of these data, it is not possible to define specific attributes of their morphology that can be used to identify interspecifc differences between fossil and Recent vertebrae. In addition, there are no valid extinct species of *Cetorhinus* with vertebrae, to serve as a basis for comparison with extant *C. maximus*.

Gill Rakers—Gill rakers are modified mucous membrane denticles (Peyer 1968). The base is fixed to the branchial arch by connective tissues and perforated by nutrient canals along the entire basal edge. Vascular canals filled with dentinal tubes and surrounded by interosteal tissue form the base. A median vascular canal arising from the base runs up the center of the filament. Dentinal tubes, originating along the outer margin of the pulp cavity, penetrate a thick layer of pallial dentine, which, with the exception of the basal attachment surface, covers the entire gill raker. A thin pigment layer overlain by enameloid covers the outermost surface of the gill raker.

Gill rakers in *Cetorhinus maximus* are present on both sides of each of the five branchial arches. From the inner edge of each arch extends a 10-cm diameter strip of mucous membrane (LACM 35876-1), and to either side of this lies a single continuous row of gill rakers with their free ends (filaments) directed towards the mouth. The semilunar base of each gill raker is attached to the mucous membrane of the gill arch. The longest gill rakers occur near the center of the arc and are about 9 cm long in the LACM specimen. They are spaced at about 12–13 per centimeter and decrease in length toward either end of the gill arch. Bigelow & Schroeder 1948:150) estimated the number of gill rakers in one series on one branchial arch to be 1260. Matthews and Parker (1950:564) estimated the total number to be from 1200 to 1300 on the anterior larger gill arches and from 1000 to 1100 on the shorter arches.

Van Den Bosch (1984), Hovestadt and Hovestadt-Euler (2011), and Welton (2013) figure gill rakers from Recent *Cetorhinus maximus*, representing central through distal positions along the gill arch, from individuals of both sexes, and a range of body lengths. Comparison of *C. maximus* gill rakers having the same relative position on the gill arch, but from individuals ranging in size from 360 cm (TL) to greater than 600 cm (TL), shows a morphologic (ontogenetic) trend with increasing body length (Hovestadt and Hovestadt-Euler, 2011). Ontogenetic changes in the morphology of *C. maximus* gill rakers from a central position on the gill arch, include: an increase in gill raker length, a shift in the basal angle from rounded to subangular, an increase in length of the medial process, and development of a concave mesial edge to the medial process. Variable attributes include degree of filament curvature at its base, basal width, and bight angles that range from curved to angular. It is possible that sexual dimorphism, or individual variation, might explain some differences in gill raker morphology; however, the sample size is too small to test this hypothesis.

Large adult *Cetorhinus maximus* gill rakers exceed 20 cm in total length (TL), whereas the most complete Empire gill raker is 2.6 +cm (Fig. 6c). Comparing the Empire gill raker bases (Fig. 6a-d) with the approximately equal sized *C. maximus* gill raker bases shown in the series illustrated by Hovestadt and Hovestadt-Euler (2011, p. 79, fig. 9, m-u, from a 672 cm (TL) female) I estimate that the Empire gill rakers shown in Figure 6, if complete, would have total lengths ranging from a minimum of five cm (Fig. 6a) to a maximum of about eight cm (Fig. 6d). These estimates are derived using a ratio of base height to gill raker length, established on the Hovestadt and Hovestadt-Euler (2011) figured gill rakers (fig. 9m-u), and applied to the Empire specimens. The Empire gill rakers (Fig. 6a-d) compare favorably with those adult *C. maximus* (Hovestadt-Hovestadt-Euler, 2011, p. 79, fig. 9m-u) in having moderately to strongly curved filament bases, and relatively flat to weakly convex distal protuberances. The basal margins are moderately long, and the medial processes are very long and narrow with weakly concave to weakly convex medial edges. Basal heights are moderately high, and basal angles are rounded to subangular. Bights are moderately wide and all appear to be subangular. Trends from a distal to central position on the gill arch include increasing curvature of the filament base, increasing basal length, increasing length of the medial process, development of a concave mesial edge of the medial process in the most central gill rakers, and an increase in gill raker length, with the longest gill rakers either in the central-most position on the gill arch (Hovestadt and Hovestadt-Euler, 2011) or just distal to the central position (Welton, 2013, fig. 12, LACM 35876-1). The Empire gill rakers differ from those of LACM 35876-1 (Welton, 2013, fig. 12) in having subangular rather than rounded bights, less curvature at the filament base, and in some gill rakers, and a less rounded mesial edge of the medial process. The gill raker sequence illustrated in Figure 6a-d approximates distal-most to central-most positions on the gill arch.

The Empire *Cetorhinus* gill rakers and vertebrae differ significantly from those of the *Keasius taylori* (Welton, 2013) and *K. parvus* (Hovestadt and Hovestadt-Euler, 2011; LACM 154925), by having much larger gill rakers, from *K. parvus* in having less curvature at the filament just above it attachment with the base, and from both *K. parvus* and *K. taylori* in having a less robust base with a much longer and narrower medial process, a more horizontal basal edge of the base, a subangular to rounded basal angle, subangular to rounded bight, and relatively short basal height. The Empire vertebrae are large and have well developed concentric lamellae. The vertebrae of *K. taylori* and *K. parvus* are much smaller and lack concentric lamellae (Welton, 2013).

Estimated Total Length of the Empire Formation Basking Shark—The total length of the Empire basking shark can be estimated using vertebral size (Natanson et al., 2008) and gill raker length (Hovestadt and Hovestadt-Euler, 2011). In the absence of a complete Empire skeleton, maximum vertebral dorsoventral heights and gill raker lengths in this individual are unknown. Assuming there were larger vertebrae and gill rakers in the shark, total length estimates based on the preserved vertebrae and gill rakers are conservative. The largest Empire centrum measures about 80 mm in dorsoventral height. According to a graph correlating vertebral dimensions to total length for Recent *Cetorhinus maximus* (Natanson et al., 2008, p. 272, fig. 2), the Empire basking shark has an estimated total length of about 450 cm. Using a correlation of gill raker length to total length of *C. maximus* (Hoevestadt and Hovestadt-Euler, 2011, p. 80, fig. 11), an 80 mm Empire gill raker (TL estimated above) correlates with a 575 cm (TL) shark.

Comments on the Use of Vertebrae, Gillrakers and Teeth in Fossil Cetorhinid Taxonomy—All nominal fossil species of *Cetorhinus* are based on gill rakers or vertebrae.

The issues related to the use of vertebrae in defining new species have been noted above, and most of the same problems apply to the use of gill rakers in taxonomy. Recent studies of extant *C. maximus* (Van Den Bosch, 1984; Hovestadt-Hovestadt-Euler, 2011; Welton, 2013) provide significant new data on gill raker morphology, and especially changes in their shape with age and position on the gill arch. However, additional work is needed to document individual, ontogenetic, perhaps sexual, and geographic variation in gill raker morphology. The use of gill rakers in fossil cetorhinid taxonomy is further complicated by the fact that some undescribed Neogene *Cetorhinus* have gill rakers very much like Recent *C. maximus*, but teeth that are distinct and warrant assignment to a new species (Welton, unpublished data).

Identification of the Empire *Cetorhinus* would have been greatly facilitated with oral teeth, but none were found with the fossil, and to my knowledge, no teeth of *Cetorhinus* have been collected from the Coos Conglomerate. Although gill rakers and vertebrae from the Empire Formation compare favorably with those of the Recent basking shark *C. maximus*, a definitive identification requires dentition.

Fossil Record of the Genus *Cetorhinus* in Oregon and California—The fossil record of the genus *Cetorhinus* in Oregon and California ranges from early Miocene through Pleistocene (Long, 1994; Welton, unpublished data). Based primarily on teeth, and to a lesser extent gill rakers and vertebrae, early and middle Miocene *Cetorhinus* from the eastern North Pacific are morphologically distinct from *C. maximus*, and represent undescribed species (Welton, unpublished data). The occurrence of *Cetorhinus* cf. *C. maximus* in the late Miocene of Oregon (Long, 1994; this study) is consistent with other late Miocene records of the species in California (Long, 1994) and Chile (Long, 1993).

Conclusions

1. A calcareous sandstone concretion containing three vertebrae and 11 fragmentary gill rakers belonging to the genus *Cetorhinus* Blainville, 1816, was collected from the Coos Conglomerate Member of the late Miocene Empire Formation, Coos County, Oregon.
2. Taphonomic data suggest the vertebrae and gill rakers represent an associated but disarticulated skeleton from one individual. The skeleton shows evidence of transport prior to deposition.
3. The Empire *Cetorhinus* gill rakers and vertebrae differ significantly from those of the *Keasius taylori* and *K. parvus,* and compare favorably with those of the Recent basking shark *C. maximus*.
4. The total length of the Empire basking shark is estimated to be between 4.5 and 5.75+ m based on correlations of vertebral and gill raker dimensions with the total length for Recent *C. maximus*.
5. Although the gill rakers and vertebrae from the Empire Formation compare favorably with those of the Recent basking shark *Cetorhinus maximus*, a definitive identification requires dentition.
6. Based primarily on teeth, and to a lesser extent gill rakers and vertebrae, early and middle Miocene *Cetorhinus* from the eastern North Pacific are distinct from *C. maximus* (Welton, unpublished data). The occurrence of *Cetorhinus* cf. *C. maximus* in the late Miocene Empire Formation of Oregon (Long, 1994; this study), is consistent with other late Miocene records of the species in California

(Long, 1994) and Chile (Long, 1993), and suggests that *C. maximus* may range no earlier than late Miocene in the eastern North Pacific.

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Literature Cited

Addicott, W.O. 1976. Neogene molluscan stages of Oregon and Washington. Pp. 95–115 in Neogene Symposium. (A.E. Fritsche, TerBest, H. Jr., and Wornardt, W.W., eds.), Society of Economic Paleontologists and Mineralogists, Pacific Section, San Francisco, California, April 1976.

———. 1981. Significance of pectinids in Tertiary biochronology of the Pacific Northwest. Pp. 95–115 in Pacific Northwest Cenozoic Biostratigraphy. (J.M. Armentrout, ed.), Geological Society of America, Special Paper 184.

Applegate, S.P. 1978. Phyletic Studies; Part 1; Tiger Sharks. Universidad Nacional Autonoma de Mexico, Instituto de Geologia, Revista, 2:55–64.

Armentrout, J.M. 1973. Molluscan paleontology and biostratigraphy of the Lincoln Creek Formation, late Eocene-Oligocene, southwestern Washington [Ph.D. dissert.]. Seattle, University of Washington, 478 pp.

———. 1980. Field trip road log for the Cenozoic stratigraphy of Coos Bay and Cape Blanco, southwestern Oregon. Pp. 175–216 in Geologic Field Trips in Western Oregon and Southwestern Washington. (K.F. Oles, Johnson, J.G., Niem, A.R., and Niem, W.A., eds.), Geologic Field Trips in Western Oregon and Southwestern Washington, State of Oregon, Department of Geology and Mineral Industries, Bulletin 101.

———. 1981. Correlation and ages of Cenozoic chronostratigraphic units in Oregon And Washington. Pp. 137–148 in Pacific Northwest Cenozoic Biostratigraphy. (J.M. Armentrout, ed.), Geological Society of America, Special Paper 184.

———, Hull, D.A., Beaulieu, J.D., and Rau, W.W. 1983. Correlation of Cenozoic stratigraphic units of western Oregon and Washington. Oregon Department of Geology and Mineral Industries, Oil and Gas Investigation 7, 90 pp.

Barnes, L.G. 2008. Miocene and Pliocene Albireonidae (Cetacea, Odontoceti), rare and unusual fossil dolphins from the Eastern North Pacific Ocean. Natural History Museum of Los Angeles County, Contributions in Science, Series, 41:99–152.

Barron, J.A. and Armentrout, J.M. 1980. Late Miocene diatom florules of the Empire Formation, Coos Bay, Oregon. Geological Society of America, Abstracts with Program, 12:95–96.

———. 1981. Marine diatom biostratigraphy of the Montesano Formation near Aberdeen, Washington. Pp. 113–126 in Pacific Northwest Cenozoic Biostratigraphy. (Armentrout, J.M., ed.), Geological Society of America, Special Paper 184.

Barthelt, D., Fejfar, O., Pfeil, F.H., and Unger, E. 1991. Notizen zu einem Profil der Selachier-Fundstelle Walbertsweiler im Bereich der miozänen Oberen Meeresmolasse Süddeutschlands. Münchner Geowissenschaftliche Abhandlungen, (A), 19:195–208.

Baut, J.-P. 1993. Contribution à l'étude des élasmobranches oligocènes du Bassin de Paris. 1, Révision des Élasmobranches du Stampien (Oligocène inférieur) de la région d'Étampes, Essonne, France. Cossmanniana, Hors-série, 2:1–12.

——— and Genault, B. 1999. Les Elasmobranches des Sables de Kerniel (Rupélien), à Gellik, Nord Est de la Belgique. Memoirs of the Geological Survey of Belgium, 45:1–61.

Berg, L.S. 1958. System der Rezenten und Fossilen Fischartigen und Fische. Hochschulbücher für Biologie, Berlin. 310 pp.

Bienkowska-Wasiluk, M. and Radwanski, A. 2009. A new occurrence of sharks in the Menilite Formation (Lower Oligocene) from the Outer (Flysch) Carpathians of Poland. Acta Geologica Polonica, 59: 235–243.

Bigelow, H.B. and Schroeder, W.C. 1948. Fishes of the Western North Atlantic. Memoir of the Sears Foundation for Marine Research, 1(1): 56–576.

Blainville, H.M.D. de. 1816. Prodrome d'une nouvelle distribution sytématique du règne animal. Bulletin des Sciences, par la Société Philomatique de Paris, 8:105–124.

Boessenecker, R.W. 2011. A new marine vertebrate assemblage from the late Neogene Purisima Formation in central California, part I: fossil sharks, bony fish, birds, and implications for the age of the Purisima Formation west of the San Gregorio fault. PalArch's Journal of Vertebrate Paleontology, 8:1–30.

Bolliger, T., Kindlimann, R., and Wegmuller, U. 1995. Die marinen Sedimente (jüngere OMM, St. Galler-Formation) am Südwestrand der Hörnlischüttung (Ostschweiz) und die palökologische Interpretation ihres Fossilinhaltes. Eclogae Geologicae Helvetiae, 88:885–909.

Bracher, H. and Unger, E. 2007. Untermiozane Haie und Rochen. Altheim, 183, 107 pp.

Brzobohaty, R. and Schultz, O. 1978. Die Fischfauna des Badeniens. Pp. 441–465 In M4 Badenien (Moravien, Wielicien, Kosovien). (A. Papp, Cicha, I., Senes, J., Steininger, F., and Mitarbeiter, eds.), Chronostratigraphie und Neostratotypen, Miozän der Zentralen Paratethys, 6.

Cappetta, H. 1987. Handbook of Paleoichthyology, Vol. 3B: Chondrichthyes II. Gustav Fischer Verlag, Stuttgart 1987, 193 pp.

———. 2006. Elasmobranchii Post-Triadici (Index specierumet generum). *In*: Fossilium Catalogus I: Animalia. (W. Riegraf, ed.), pt. 142, Leiden, Backhuys Publishers, 472 pp.

——— and Nolf, D. 1991. Les sélaciens du Pliocène inférieur de Le-Puget-sur-Argens (Sud-Est de la France). Palaeontographica, Abt. A, 218:49–67.

Cicimurri, D.J. and Knight, L.J. 2009. Late Oligocene sharks and rays from the Chandler Bridge Formation, Dorchester County, South Carolina, USA. Acta Palaeontologica Polonica, 54: 627–647.

Cigala-Fulgosi, F., Casati, S., Orlandini, A., and Persico, D. 2009. A small fossil fish fauna, rich in *Chlamydoselachus* teeth, from the Late Pliocene of Tuscany (Siena, central Italy). Cainozoic Research, 6:3–23.

Cione, A.L. and Reguero, M.A. 1998. A middle Eocene basking shark (Lamniformes, Cetorhinidae) from Antarctica. Antarctic Science, 10:83–88.

Compagno, L.J.V. 1973. Interrelationships of living elasmobranchs. Pp. 15–61 in Interrelationships of Fishes. (P.H. Greenwood, Miles, R.S., and Patterson, C., eds.), Zoological Journal of the Linnean Society, 53 (Supplement 1).

———. 1984. FAO Species Catalogue: Sharks of the world, Part 1 – Hexanchiformes to Lamniformes. FAO Fisheries Synopsis No. 125, 4:1–249.

———. 2001. Sharks of the world, an annotated and illustrated catalog of shark species known to date; v. 2, bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). FAO Species Catalog for Fishery Purposes, 2, 269 pp.

Cuny, G. 1995. French vertebrate faunas and the Triassic-Jurassic boundary. Palaeogeography, Palaeoclimatology, Palaeoecology, 119:343–358.

———, Hunt, A., Mazin, J.-M., and Rauscher, R. 2000. Teeth of enigmatic neoselachian sharks and an ornithischian dinosaur from the uppermost Triassic of Lons-le-Saunier (Jura, France). Paläontologische Zeitschrift, 74:171–185.

———, Mazin, J.-M., and Rauscher, R. 1994. Saint-Germain-les-Arlay: un nouveau site rhétien daté par la palynologie et l'étude des vertébrés dans le département du Jura (France): Revue de Paléobiologie, 14:Pp. 35–48.

Dall, W.H. 1898. A table of North American Tertiary formations, correlated with one another and with those of western Europe, with annotations. U. S. Geol. Surv. 18th Ann. Rept., 2:327–348.

———. 1909. Contributions to the Tertiary paleontology of the Pacific coast, I. The Miocene of Astoria and Coos Bay, Oregon. United States Geological Survey Professional Paper 59, 278 pp.

De Pietri, V., Berger, J.-P., Pirkenseer, C., Scherler, L., and Mayr, G. 2010. New skeleton from the early Oligocene of Germany indicates a stem-group position of diomedeoidid birds. Acta Palaeontologica Polonica, 55:23–34.

Diller, J.S. 1896. A geological reconnaissance in northwestern Oregon. United States Geological Survey 17th Annual Report, pt. 1:441–520.

Domning, D.P. 1978. Sirenian evolution in the North Pacific Ocean. University of California Publications in Geological Sciences, 18:1–176.

Duffin, C.J. 1998. New shark remains from the British Rhaetian (latest Triassic). 1. The earliest basking shark. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, 1998:157–181.

Dutheil, D.B. 1991. A checklist of Neoselachii (Pisces, Chondrichthyes) from the Palaeogene of the Paris Basin, France. Tertiary Research, 13:27–36.

Fitch, J.E. 1970. Fish remains, mostly otoliths and teeth, from the Palos Verdes Sand (late Pleistocene) of California. Natural History Museum of Los Angeles County, Contributions in Science, n. 199, 14 pp.

Freess, W.B. 1991. Elasmobranchii und Teleostei des Sternberger Gesteins (Oberoligozän). Archiv für Geschiebekunde, 1:131–216.

———. 1992. Haie, Rochen und Chimären aus dem mitteloligozänen Meeressand von Leipzig. Aufschluss, 43:195–214.

Frohlicher, H. and Weiler, W. 1952. Die Fischfauna der unterstampischen Molasse des Entlebuchs, Kt. Luzern, und ihre paläogeographische Bedeutung. Eclogae Geologicae Helvetiae, 45:1–35.

Genault, B. 1993. Contribution à l'étude des élasmobranches oligocènes du Bassin de Paris. 2: Découverte de deux horizons à Elasmobranches dans le Stampien (Sables de Fontainebleau) de la feuille géologique de Chartres. Cossmanniana, Hors-série, 2:13–36.

Gill, T. 1862. Analytical synopsis of the Order of Squali and revision of the nomenclature of the genera. Annals of the Lyceum of Natural History of New York, 7:367–408.

Gille, D., Gille, A., and Fichter, J. 2010. Verbreitung und Zusammensetzung der Elasmobranchierfauna im Kasseler Meeressand (Ober-Oligozän, Chattium, Kassel-Formation) Nordhessen, insbesondere im Ahnetal bei Kassel (GK 25, Bl. 4622 Kassel West). Geologisches Jahrbuch Hessen, 136: 5–33.

Godefroit, P., Cuny, G., Delsate, D., and Roche, M. 1998. Late Triassic vertebrates from Syren (Luxembourg). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 210:305–343.

Gonzalez-Barba, G. and Thies, D. 2000. Asociaciones faunisticas de condrictios en el Cenozoico de la Peninsula de Baja California, Mexico. Profil, 18:1–4.

Gottfried, M.D. 1995. Miocene basking sharks (Lamniformes: Cetorhinidae) from the Chesapeake Group of Maryland and Virginia. Journal of Vertebrate Paleontology, 15:443–447.

Gunnerus, J.E. 1765. Brugden (*Squalus maximus*), Beskrvenen ved J. E. Gunnerus. Det Trondhiemske Selskabs Skrifter, 3:33–49.

Hasse, J.C.F. 1879–1885(1882). Das Naturliche System der Elasmobranchier auf Grundlage des Baues und der Entwicklung ihrer Wirbelsaule. Eine Morphologische und Palaontologische Studie: Gustav Fischer Verlag, Jena. Allgemeiner Theil. i–vi:1–76, 1879; besonderer Theil, (1): 94 pp, pls. 1–12, 1882; (2):97–109, pls. 13–23, 1882; (3): i–vi:183–285, pls. 24–40, 1882; Erganzungsheft: 27 pp.

Haye, T., Reinecke, T., Gurs, K., and Piehl, A. 2008. Die Elasmobranchier des Neochattiums (Oberoligozän) von Johannistal, Ostholstein, und Ergänzungen zu deren Vorkommen in der Ratzeburg-Formation (Neochattium) des südöstlichen Nordseebeckens. Palaeontos, 14:55–97.

Herman, J. 1979. Réflexions sur la systématique des Galeoidei et sur les affinités du genre *Cetorhinus* à l'occasion de la découverte d'éléments de la denture d'un exemplaire fossile dans les sables du Kattendijk à Kallo (Pliocène Inférieur, Belgique). Annales de la société géologique de Belgique, 102:357–377.

———, Crochard, M., and Girardot, M. 1974. Quelques restes de sélaciens récoltés dans les sables du Kattendijk à Kallo. I. Selachii – Euselachii. Bulletin de la Société Belge de Géologié, 83:15–31.

Hovestadt, D.C. and Hovestadt-Euler, M. 2011. A partial skeleton of *Cetorhinus parvus* Leriche, 1910 (Chondrichthyes, Cetorhinidae) from the Oligocene of Germany. Paläontologische Zeitschrift, 86: 71–83.

———, ———, and Micklich, N. 2010. A review of the chondrichthyan fauna of Grube Unterfeld (Frauenweiler) clay pit. Kaupia, 17:57–71.

Howe, H.V.W. 1922. Faunal and stratigraphic relationships of the Empire formation, Coos Bay, Oregon. California University, Department of Geological Sciences Bulletin, 14:85–114.

Huxley, T.H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia. Proceedings of the Zoological Society of London, 1880: 649–662.

Jonet, S. 1947. Présence d'un Squale du genre *Cetorhinus* dans l'Oligocène de Roumanie. Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie, 56:17–19.

Jordan, D.S. 1923. A classification of fishes including families and genera as far as known. Stanford University Publications (Biological Sciences), 3:77–243.

——— and Hannibal, H. 1923. Fossil sharks and rays of the Pacific slope of North America. Bulletin of the Southern California Academy of Sciences, 22:27–68.

Kanakoff, G. 1956. Fish records from the Pleistocene of southern California. Bulletin of the Southern California Academy of Sciences, 55:47–49.

Karasawa, H. 1989. Late Cenozoic elasmobranchs from the Hokuriku district, central Japan. The Science Reports of Kanazawa University, 34:1–57.

Kikuchi, Y. and Takaoka, Y. 1979. Discovery of the fossil gill raker of a basking shark from the Tertiary system in Chichibu Basin, Saitama Prefecture. Journal of the Geological Society of Japan, 85:97–98.

Kruckow, T. 1961. Miocäne Selachier-Faunen in nordwestdeutschen Randgebieten der Nordsee. Meyniana, 10:42–48.

Lamb, A. and Edgell, P. 2010. Coastal fishes of the Pacific Northwest; 2nd ed.. Harbour Publishing Co. Ltd., Madeira Park, British Columbia. 335 pp.

Landini, W. 1977. Revizione degli «*Ittiodontoliti pliocenici*» della collezione Lawley. Palaeontographia Italica, 70:92–134.

Langenwalter, P.E. 1975. Chordates: The fossil vertebrates of the Los Angeles – Long Beach harbors region. Pp. 36–54 in Marine studies of San Pedro Bay, California. (D.F. Soule and Oguri, M., eds.), Part 9, Paleontology. Allen Hancock Foundation, Harbors Environmental Projects and The Office of Sea Grant Programs, University of Southern California, Los Angeles, USC-SG-4-75.

Lawley, R. 1876. Nuovi studi sopra ai pesci ed altri vertebrati fossili delle Colline Toscane. Firenze, Tipografia dell Arte della Stampa, 1–122.

Leriche, M. 1908. Sur un appareil fanonculaire de *Cetorhinus* trouvé à l'état fossile dans le Pliocène d'Anvers. Comptes Rendus hebdomadaires des séances de l'Academie des Sciences, 146:875–878.

———. 1910. Les poissons tertiaires de la Belgique. III. Les poissons oligocènes. Mémoires du Musée Royal d'Histoire Naturelle de Belgique, 5:229–363.

———. 1921. Sur les restes de Poissons remaniés dans le Néogène de la Belgique. Leur signification au point de vue de l'histoire géologique de la Belgique pendant le tertiaire supérieur. Bulletin de la Société Belge de Géologié, 30:115–120.

———. 1948. Note sur les rapports entre la faune ichthyologique de l'Argile à septaria (Septarienton) du bassin de Mayence et celle de l'Argile de Boom (Rupelien moyen), suivie d'observations nouvelles sur quelques-unes des espèces communes aux deux faunes. Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie, 57:176–185.

Long, D.J. 1993. Late Miocene and early Pliocene fish assemblages from the north coast of Chile. Tertiary Research, 17:117–126.

———. 1994. Historical biogeography of sharks from the eastern North Pacific Ocean. Ph.D. Dissertation, Department of Integrative Biology, University of California, Berkeley, 371 pp.

Malyshkina, T. 2006. Elasmobranchs of the western margin of the West Siberian Paleogene basin. Ekaterinburg. 224 pp.

Marsili, S. 2008. Systematic, paleoecologic and paleobiogeographic analysis of the Plio-Pleistocene Mediteranean elasmobranch fauna. Atti Societa Toscana Scienze Naturali, Serie A, 113:81–88.

Matthews, L.H. and Parker, H.W. 1950. Notes on the anatomy and biology of the basking shark (*Cetorhinus maximus* (Gunner)): Proceedings of the Zoological Society of London, 120:535–576.

Mecklenburg, C.W., Mecklenburg, T.A., and Thorsteinson, L.K. 2002. Fishes of Alaska. American Fisheries Society, Bethesda, Maryland. 1116 pp.

Merle, D., Baut, J.-P., Ginsburg, L., Sagne, C., Hervet, S., Carriol, R.-P., Venec-Peyre, T., Blanc-Valleron, M., Mourer-Chauviret, C., Arambol, D., and Viette, P. 2002. Découverte d'une faune de vertébrés dans l'Oligocène inférieur de Vayres-sur-Essonne (bassin de Paris, France): biodiversité et paléoenvironnement. Comptes Rendus Palevol, 1:111–116.

Mitchell, E. and Tedford, R.H. 1973. The Enaliarctinae, a new group of extinct aquatic Carnivora and a consideration of the origin of the Otariidae. Bulletin of the American Museum of Natural History, 151:203–284.

Muller, A. 1976. Beiträge zur Kenntnis der Fauna des Rupels der südlichen Leipziger Tieflandbucht. Teil I: Die Selachier des Leipziger Rupels. Abhandlungen und Berichte des Naturkundlichen Museums Mauritianum Altenburg, 9:83–117.

———. 1983. Fauna und Palökologie des marinen Mitteloligozäns der Leipziger Tieflandsbucht (Böhlener Schichten). Altenburger naturwissenschaftliche Forschung, 2, 152 pp.

Muller, J. and Henle, F.G.J. 1837. Gattungen der Haifische und Rochen nach einer von ihm mit Hrn. Henle unternommenen gemeinschaftlichen Arbeit über die Naturgeschichte der Knorpelfische. Berichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin, 1837:111–118.

Natanson, L.J., Wintner, S.P., Johansson, F., Piercy, A., Campbell, P., De Maddalena, A., Gulak, S.J.B., Human, B.A., Cigala-Fulgosi, F., Ebert, D.A., Hemida, F., Mollen, F.H., Vanni, S., Burgess, G.H., Compagno, L.J.V., and Wedderburn-Maxwell, A. 2008. Ontogenetic vertebral growth patterns in the basking shark *Cetorhinus maximus*. Marine Ecology Progress Series, 361:267–278.

Noetling, F. 1885. Die Fauna des samländischen Tertiärs. Abhandlungen zur geologischen Specialkarte von Preussen und den Thüringischen Staaten, 6, 218 pp.

Nolf, D. 1986. Haaie- en Roggentanden uit het Tertiair van Belgie. Institut royal des Sciences naturelles de Belgique, 1–171.

Olson, H.C. and Welton, B.J. 1986. Foraminifera and fishes of Tertiary units in the Bakersfield, California area. Pp. 47–49 in American Association of Petroleum Geologists, Pacific Section Guidebook. (P. Bell, ed.), Bakersfield, California.

Pfeil, F.H. 1981. Eine nektonische Fischfauna aus dem unteroligozänen Schönecker Fischschiefer des Galon-Grabens in Oberbayern. Geologica Bavarica, 82:357–388.

Pharisat, A. 1998. Marine fish biodiversity in the Oligocene of Froidefontaine (Belfort Territory, France). Italian Journal of Zoology, 65:189–191.

Peyer, B. 1968. Comparative odontology. (Zangrel, R., ed.), Chicago University Press, 347 pp.

Purdy, R.W., Schneider, V.P., Applegate, S.P., McLellan, J.H., Meyer, R.L., and Slaughter, B.H. 2001. The Neogene sharks, rays, and bony fishes from Lee Creek Mine, Aurora, North Carolina, III. Pp. 71–202 in Geology and Paleontology of the Lee Creek Mine, North Carolina. (C.E. Ray and Bohaska, D.J., eds.), Smithsonian Contributions to Paleobiology, 90.

Reinecke, T., Louwye, S., Havekost, U., and Moths, H. 2011. The elasmobranch fauna of the late Burdigalian, Miocene, at Werder-Uesen, Lower Saxony, Germany, and its relationships with Early Miocene faunas in the North Atlantic, Central Paratethys and Mediterranean. Palaeontos, 20: 1–170.

———, Moths, H., Grant, A., and Breitkreuz, H.. 2005. Die Elasmobranchier des norddeutschen Chattiums, insbesondere des Sternberger Gesteins (Eochattium, Oligozän). Palaeontos, 8:1–135.

———, Stapf, H., and Raisch, M. 2001. Die Selachier und Chimären des Unteren Meeressandes und Schleichsandes im Mainzer Becken (Rupelium, Unteres Oligozän). Palaeontos, 1:1–73.

———, Von Der Hocht, F., and Gurs, K. 2008. Die Elasmobranchier des Vierlandiums, Unteres Miozän, im Nordwestdeutschen Becken aus Bohrungen und glaziofluviatilen Geröllen (‘‘Holsteiner Gestein’’) der Vierlande-Feinsande (Holstein) und der Kakert-Schichten (Niederrhein). Palaeontos, 14:1–54.

Ridewood, W.G. 1921. On the calcification of the vertebral centra in sharks and rays. Philosophical Transactions of the Royal Society of London, Series B, Containing Papers of a Biological Character, 210:311–407.

Schmid, H.-P., Harzhauser, M., Kroh, A., Coric, S., Rogl, F., and Schultz, O. 2001. Hypoxic events on a middle Miocene carbonate platform of the central paratethys (Austria, Badenian, 14 Ma). Annalen des Naturhistorischen Museums in Wien, 102A:1–50.

Schultz, O. 1978. Neue und fehlinterpretierte Fischformen aus dem Miozän des Wiener Beckens. Annalen des Naturhistorischen Museums in Wien, 81:203–219.

———, Brzobohaty, R., and Kroupa, O. 2010. Fish teeth from the Middle Miocene of Kienberg at Mikulov, Czech Republic, Vienna Basin. Annalen des Naturhistorischen Museums in Wien, 112A: 489–506.

Smith, A. 1828. Descriptions of new, or imperfectly known objects of the animal kingdom, found in the south of Africa. South African Commercial Advertiser, 3, 2 pp.

Springer, S. and Gilbert, P.W. 1976. The basking shark, *Cetorhinus maximus*, from Florida and California, with comments on its biology and systematics. Copeia, 1:47–54.

Stewart, J.D. 1997. New late Miocene fishes from the Almejas Formation of Cedros Island, Baja California. Memoirs of the Fourth International Meeting on Geology of the Baja California Peninsula. (Unpaginated).

Tomita, T. and Oji, T. 2010. Habitat reconstruction of Oligocene elasmobranchs from Yamaga Formation, Ashiya Group, western Japan. Paleontological Research, 14:69–80.

Uyeno, T. and Matsushima, Y. 1974. Early Pleistocene remains of basking shark, hammerhead shark, and others found in Yokohama, Japan. Bulletin of the Kanagawa Prefectural Museum, Natural Science, 7:57–66.

———, Ono, K., and Sakamoto, O. 1983. Miocene elasmobranchs from Chichibu Basin, Saitama, Japan. Bulletin of the Saitama Museum of Natural History, 1:27–36.

———, Yabumoto, Y., and Kuga, N. 1984. Fossil fishes of Ashiya Group. I. Late Oligocene elasmobranches from Islands of Ainoshima and Kaijima, Kitakyushu. Bulletin of the Kitakyushu Museum of Natural History, 5:135–142.

Van Beneden, P.-J. 1871. Recherches sur quelques poissons fossiles de Belgique. Bulletin de l'Academie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique, 31(Serie 2): 493–518.

Van Den Bosch, M. 1981. Elasmobranchii from limonitic sandstone of Siadlo Górne near Szczecin, Poland. Mededelingen Van De Werkgroep Voor Tertiaire En Kwartaire Geologie, 18:127–131.

———. 1984. Oligocene to Recent Cetorhinidae (Vertebrata, basking sharks); problematical finds of teeth, dermal scales and gill-rakers. Mededelingen Van De Werkgroep Voor Tertiaire En Kwartaire Geologie, 21:205–232.

Van Der Brugghen, W. 2005. Over fossiele resten van *Cetorhinus* cf. *maximus* uit het Plioceen van Kallo (België). Grondboor en Hamer, 1:8–12.

Vialle, N., Adnet, S., and Cappetta, H. 2011. A new shark and ray fauna from the Middle Miocene of Mazan, Vaucluse (southern France) and its importance in interpreting the paleoenvironment of marine deposits in the southern Rhodanian Basin. Swiss Journal of Palaeontology, 130:241–258.

Von Der Hocht, F. 1978a. Bestandsaufnahme der Chondrichthyes-Fauna des Unteren Meeressandes im Mainzer Becken. Mededelingen Van De Werkgroep Voor Tertiaire En Kwartaire Geologie, 15: 77–83.

———. 1978b. Bestandsaufnahme der Chondrichthyes-Fauna des Unteren Meeressandes im Mainzer Becken. Mededelingen Van De Werkgroep Voor Tertiaire En Kwartaire Geologie, 15:163–165.

Weaver, C.E. 1945. Tertiary stratigraphy and paleontology of the Tertiary formations at Coos Bay, Oregon. Washington University. [Seattle] Pubblications in Geology, 6:31–62.

Weiler, W. 1922. Beiträge zur Kenntnis der tertiären Fische des Mainzer Beckens I. Abhandlungen der hessischen Geologischen Landesanstalt zu Darmstadt, 6:69–135.

———. 1928. Beiträge zur Kenntnis der tertiären Fische des Mainzer Beckens II. 3. Teil Die Fische des Septarientones. Abhandlungen der hessischen Geologischen Landesanstalt zu Darmstadt, 8:1–61.

———. 1931. Revision der Fischfauna des Septarientones von Wiesloch bei Heidelberg. Sitzungsberichte der Heidelberger Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, 11: 3–15.

Welton, B.J. 2013. A new archaic basking shark (Lamniformes: Cetorhinidae) from the late Eocene of western Oregon, U.S.A., and description of the dentition, gill rakers, and vertebrae of the Recent basking shark *Cetorhinus maximus* (Gunnerus). New Mexico Museum of Natural History and Science, Bulletin 58, 48 pp.

Wijnker, E., Bor, T.J., Wesselingh, F.P., Munsterman, D.K., Brinkhuis, H., Burger, A.W., Vonhof, H.B., Post, K., Hoedemakers, K., Janse, A.C., and Taverne, N. 2008. Neogene stratigraphy of the Langenboom locality (Noord-brabant, the Netherlands). Netherlands Journal of Geosciences, 87: 165–180.

Wintner, S.P. and Cliff, G. 1999. Age and growth determination of the white shark, *Carcharodon carcharias*, from the east coast of South Africa. Fishery Bulletin, 97:153–169.

———. 2000. Preliminary study of vertebral growth rings in the whale shark, *Rhincodon typus*, from the east coast of South Africa. Environmental Biology of Fishes, 59:441–451.

Woodward, A.S. 1889. Catalogue of the fossil fishes in the British Museum. Part. 1. British Museum (Natural History), 474 pp.

Yabumoto, Y. and Uyeno, T. 1994. Late Mesozoic and Cenozoic fish faunas of Japan. Island Arc, 3: 255–269.